THE VARIOUS TAXA AND HOSTS OF THE NORTH AMERICAN
CELASTRINA (LEPIDOPTERA: LYCAENIDAE)

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Abstract.—The genus *Celastrina* (Lepidoptera: Lycaenidae) includes Holarctic small
blue butterflies whose larvae feed on the flowers, fruits, leaves, and galls of a diverse
variety of plants. In North America the *Celastrina ladon* species complex presently con-
tains three recognized species (*ladon, neglectamajor,* and *nigra*). The versatile *Celastrina
ladon* consists of eight subspecies and several seasonal forms. Many of these forms are
biologically distinct allochronic races. The hosts and distributions of the species, subspe-
cies, and races of the *C. ladon* complex in North America are presented. In the West, the
Celastrina have segregated into seven subspecies, while in the East they have reached
greater evolutionary diversity and formed several species and several seasonal races. It
appears that host shifts, associated with changes in adult season or habitat preference,
may have played a major role in the historical evolution of the species and races of the
C. ladon complex.

Key Words: Host races, Lycaenopsis, distribution, asynchronous, evolution, phytoph-
agous, Polyommatini, sympatric speciation

Host plant adaptation is believed to have
had a major role in the evolution of phy-
tophagous insects (Walsh 1864, Jermy 1984,
Strong et al. 1984). Some insect host races
feature differences in rates of adult matu-
ration, which result in asynchronous mating
periods and genetic isolation (Wood and
Guttman 1983, Bush 1969, Phillips and
Barnes 1975, Knerer and Atwood 1973,
Smith 1988). Such allochronic examples
may be incipient species. Seasonal isolation
therefore may play as important a role as
host differences in the evolution of species
in sympatry (Smith 1988, Wood and Keese
1990, Wood et al. 1990).

Celastrina are small blue butterflies whose
larvae feed mainly on the flowering parts of
a broad variety of plants. Three North

American species are currently recognized:
Celastrina ladon (Cramer, *Celastrina ne-
glectamajor* Opler & Krizek, and *Celastrina
nigra* (Forbes) (= *ebenina* Clench) (see Cra-
mer 1780, Forbes 1960, Clench 1972, Opler
and Krizek 1984, Scott and Wright, in press).
These taxa are considered bonafide species,
since they exhibit discrete morphological
and host differences in sympatry. *Celastrina
nigra* larvae likewise feed exclusively on
Aruncus dioicus (Wagner and Mellichamp
1978); *C. neglectamajor* larvae feed exclu-
sively on *Cimicifuga racemosa* (Edwards
1878, 1883b); however *C. ladon* larvae feed
on a wide variety of plants (56 species, 19
families) (Scott 1986).

Eight North American subspecies of *C.
ladon* are currently recognized: *argentata*

(Fletcher), *cinerea* (Edwards), *echo* (Edwards), *gozora* (Boisduval), *ladon* (Cramer), *lucia* (Kirby), *nigrescens* (Fletcher), and *sidara* (Clench) (Miller and Brown 1981). Presently, only subspecies *ladon* and *lucia* are recognized in eastern North America. These eastern subspecies have traditionally been separated into the following seasonal forms: "lucia" (Kirby) with a dark discal patch on ventral hindwing (VHW), "marginata" (Edwards) with a dark VHW outer margin, "lucimargina" (Scott) with a dark VHW discal patch and margin, "violacea" (Edwards) with dusky gray ventral surface and prominent maculations (without darkened disc or margin on VHW), and "neglecta" (Edwards) with white ventral surface, reduced maculations, and white insuffusion into dorsal blue ground color. The spring forms ("lucia," "lucimargina," "marginata," and "violacea") can be found together which suggests that *C. ladon* is genetically variable. Some types of "violacea" and "neglecta" fly later in late spring or summer after the flights of the earlier spring forms have been completed. Since there is little seasonal overlap between the spring and summer groups and in aggregate they are polyphagous, they have been considered seasonal forms of the same species (Edwards 1883b, Miller and Brown 1981, Opler and Krizek 1984, Scott 1986).

The distributions and hosts of North American *Celastrina* (including eastern races) are poorly known. Proper data are necessary to understand *Celastrina* kinships and evolutionary histories. The purpose of this paper is to present the hosts and distributions of the species, subspecies, and races of the *C. ladon* complex, to identify areas of overlap or sympatry between races, and to present diagnostic characters which distinguish them.

Materials and Methods

Hosts were identified by observations of ovipositing females in the field and/or by rearing field collected larvae to adults. Larvae were collected by finding them in ant attendance or by beating specific plant parts into a heavy cloth net. Discrimination of adult taxa was accomplished by a table of morphological and biological characters (Table 1). The adult color patterns of many races are stable and consistent; their ranges were delineated from data accumulated by the examination of thousands of museum specimens and material contributed by collectors. Distributions of monophagous species and races were further substantiated by comparison with their host's distributions. Host data are summarized in the Appendix.

Results

North American species

The adult morphological characters and seasonal occurrences used to distinguish species of North American *Celastrina* are listed in Table 1. Of the three *Celastrina* species recognized in North America, two of these, *C. nigra* and *C. neglectamajor*, share similar ranges with density centers in the Ozarks in the Midwest and the central and southern Appalachians in the East (Figs. 1, 2). *Celastrina neglectamajor* extends further north in the Appalachians and covers 34% more area than *C. nigra*. Both *C. nigra* and *C. neglectamajor* are monophagous and their larval food plants are *Aruncus dioicus* (Rosaceae) and *Cimicifuga racemosa* (Ranunculaceae) respectively. The distributions of the food plants for *C. neglectamajor* and *C. nigra* are outlined around the ranges of the corresponding butterflies (Figs. 1, 2). Both butterflies occupy about 50% of their host's range.

Celastrina nigra and *C. neglectamajor*, unlike *C. ladon*, exhibit little geographic variability in wing pattern. *Celastrina nigra* males are distinguished from other *Celastrina* by three morphological characters: presence of long overlapping scales (replacing androconia) on the dorsal wing surface, a dark dorsal brown to black coloration, and absence of blue iridescent scales (Table 1).

Table 1. Morphological characters which distinguish the different *Celastrina* species, subspecies, and races.

Taxa	Characters*									
	MSA	DLS	DSG	DWS	DDM	VSG	VMS	VDP	VDM	RSO
neglectamajor	3, 4	0	1, 2	2	2	3	1	0	0	3
nigra (= *ebenina*)	2	1	5	0	2	2	1	0	0	2
cinerea	2	0	4	0	2	1, 2	1	0	0	1–5
gozora	2, 3	0	4	2	2	3	1	0	0	1–5
echo	2, 3	0	4	0	1	2	1	0	0	1–4
"bakeri"	2	0	4	0	1	4	1	0	0	2, 3
nigrescens	2	0	4	0	2	2	2	1	1	2, 3
sidara	2	0	2, 4	0	1	2	1, 2	0, 1	0	2, 3
argentata	2, 3	0	2	1	1	3	1	0	0	3, 4
lucia	1	0	1	0	1	1	2	1	1	1
lucia Auct.	2, 3	0	1–4	0, 1	1	2, 3	1, 2	0, 1	0, 1	1, 2
ladon										
"violacea" I	2	1	3	0	1	2	1, 2	0	0	1, 2
"violacea" II	2, 3	0	2	1	1	2, 3	1, 2	0	0	2, 3
"violacea" III	2, 3	0	2	1	1	3	1	0	0	2, 3
"neglecta"	2, 3	0	2	2	2	3	1	0	0	3–5

* MSA = maximum size of adults: 1 = small, 2 = medium, 3 = large, 4 = very large; DLS = overlapping long scales dorsal surface of male wings esp. forewings: 1 = present, 0 = absent; DSG = dorsal ground color of males: 1 = light pale blue, 2 = blue, 3 = violet-blue, 4 = purple-blue, 5 = black; DWS = white insuffusion of dorsal male blue wings: 0 = absent, 1 = present only along edges of wings and along veins, 2 = throughout the wings; DDM = dorsal dark margin on females: 1 = narrow, 2 = wide; VSG = ventral surface ground color: 1 = dark gray, 2 = light gray, 3 = white, 4 = white with greenish tint; VMS = ventral macule size: 1 = small, 2 = large; VDP = ventral discal patch on hindwing: 1 = present, 0 = absent; VDM = ventral hindwing dark margin: 1 = present, 0 = absent; RSO = relative seasonal occurrence of the adults: 1 = early spring, 2 = mid spring, 3 = late spring, 4 = early summer, 5 = late summer (occ. fall).

Females are easily distinguished by their dorsal wing surface which is generally darker (esp. borders and veins) than the other species. Males and females of *C. neglectamajor* are very often larger than other sympatric *Celastrina* and have blue dorsal scales with some degree of white insuffusion. The venter is often immaculate white with much reduced maculations (Table 1). This species can only be confused with one race of *C. ladon* ("neglecta"), which is discussed below under *C. l. ladon* races.

The third species, *C. ladon,* occurs as 8 subspecies and several races distributed throughout most of North America (Figs. 3–5) and their larvae feed on a wide variety of plants. See following sections.

Celastraina ladon subspecies

Discussions of subspecies' morphological characters are found in Cramer (1780), Kir-by (1837), Edwards (1864, 1883a), Boisduval (1870), Fletcher (1903), Clench (1944), as well as Brown (1970). The wing characters which distinguish these subspecies are summarized in Table 1. The subspecies of *C. ladon* are primarily allopatric (Figs. 3–5) and only one (*lucia*) occurs on both North American coasts and in northern latitudes which were covered by glaciers during the recent Wisconsin glaciation (Fig. 4a). The subspecies of *C. ladon* are *argentata, cinerea, echo, gozora, ladon* (as races "violacea" I, II, III and "neglecta" in Figs. 4, 5), *lucia, nigrescens,* and *sidara.*

Subspecies *cinerea* occurs throughout Arizona (except SW corner), southeastern California, southern Nevada, southern Utah, southeastern Colorado, western two-thirds of New Mexico, and northern Mexico (Fig. 3). It is replaced by *gozora* to the south in Mexico and Central America (Fig. 3a). Sub-
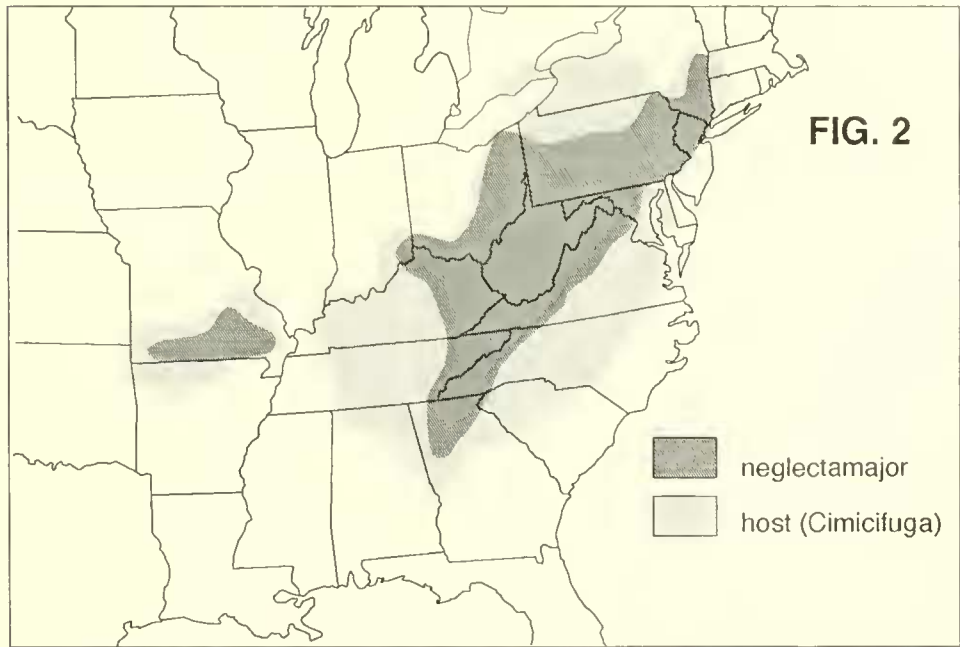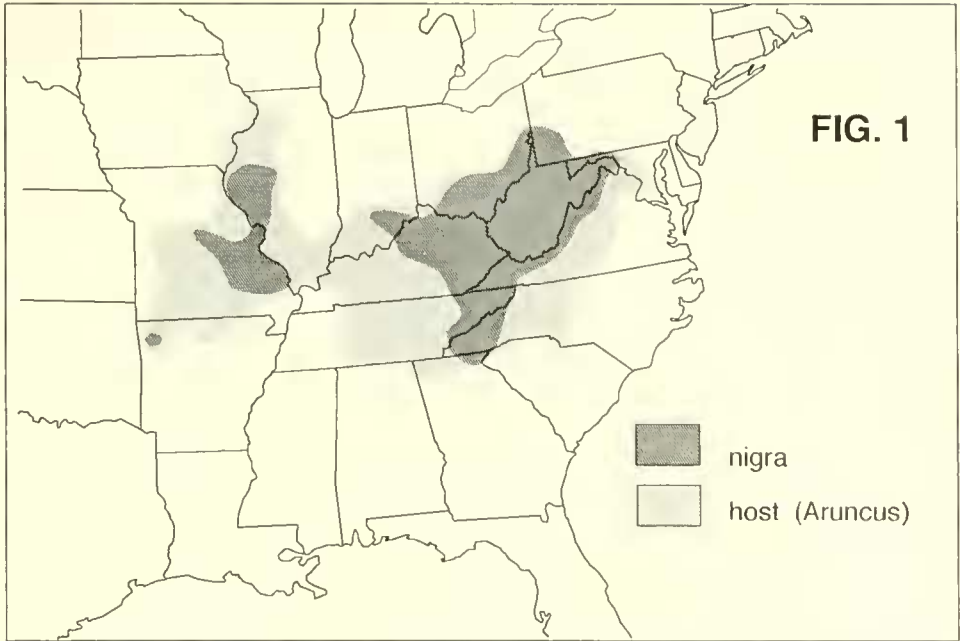
Fig. 1.   Map of eastern United States showing the geographic range of *Celastrina nigra*. The range of its host plant *Aruncus dioicus* is lightly shaded around the range of the butterfly.

Fig. 2.   Map of eastern United States showing the geographic range of *Celastrina neglectamajor*. The range of its host plant *Cimicifuga racemosa* is lightly shaded around the range of the butterfly.
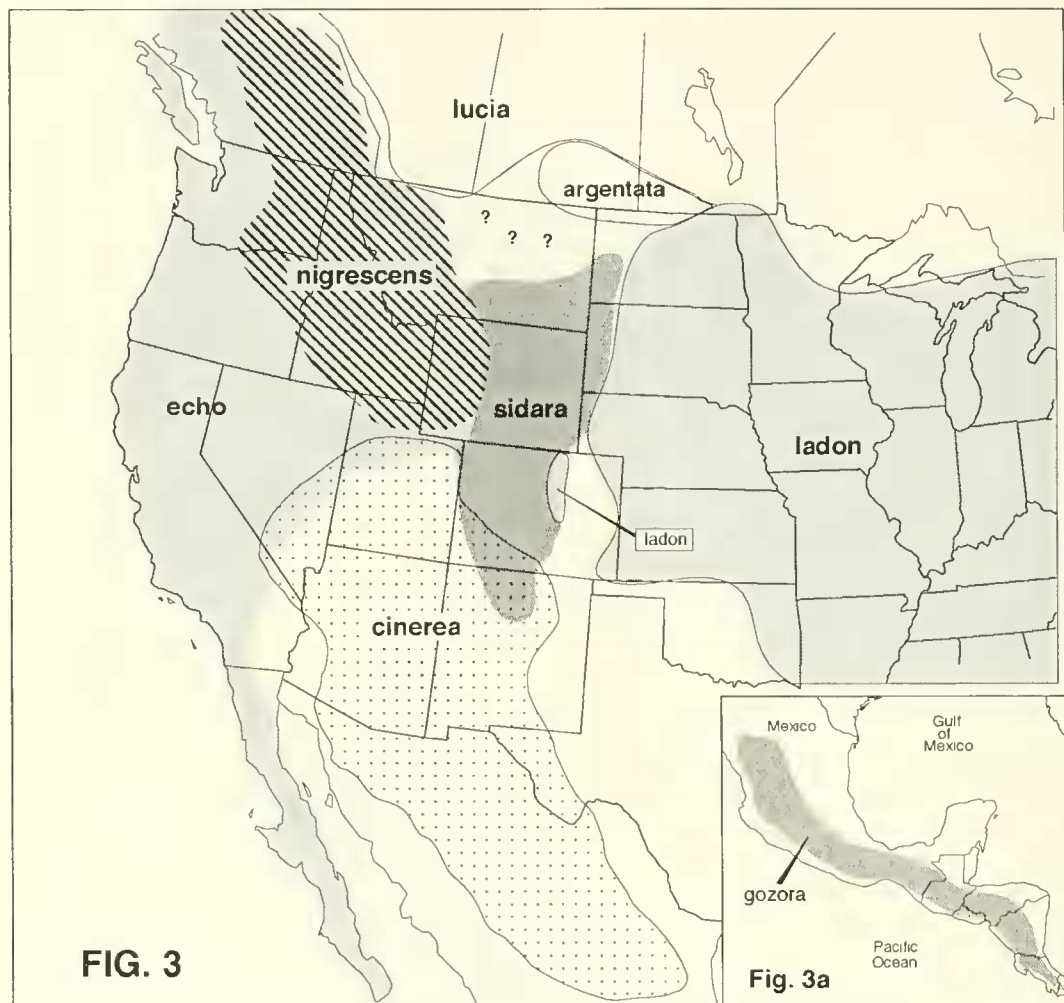
Fig. 3. Map of western North America showing the geographic ranges of the different western subspecies and of the midcontinent range of eastern ssp. *C. l. ladon.* Fig. 3a (inset) Map of Mexico and Central America showing range of subspecies *gozora.*

species *echo* occurs throughout most of California (and Baja California), Oregon, Washington, southern British Columbia, Idaho, and extends to western Montana, western Wyoming, northern Utah, and northern Nevada. *Celastrina l. echo* and *C. l. nigrescens* exhibit a broad blend zone in southern British Columbia, eastern Washington, northeastern Oregon, Idaho, western Montana, northern Utah, and western Wyoming. In this blend zone, wing char-

acters of populations range from typical *echo* to typical *nigrescens.* Individuals of subspecies *nigrescens* are quite variable and exhibit the forms "lucia," "marginata" and "violacea." Subspecies *sidara* occurs from northern New Mexico through the western two-thirds of Colorado, west to extreme northeastern Utah, and north through central and eastern Wyoming to southern Montana, the Black Hills of South Dakota, and the Badlands in southwestern North Da-
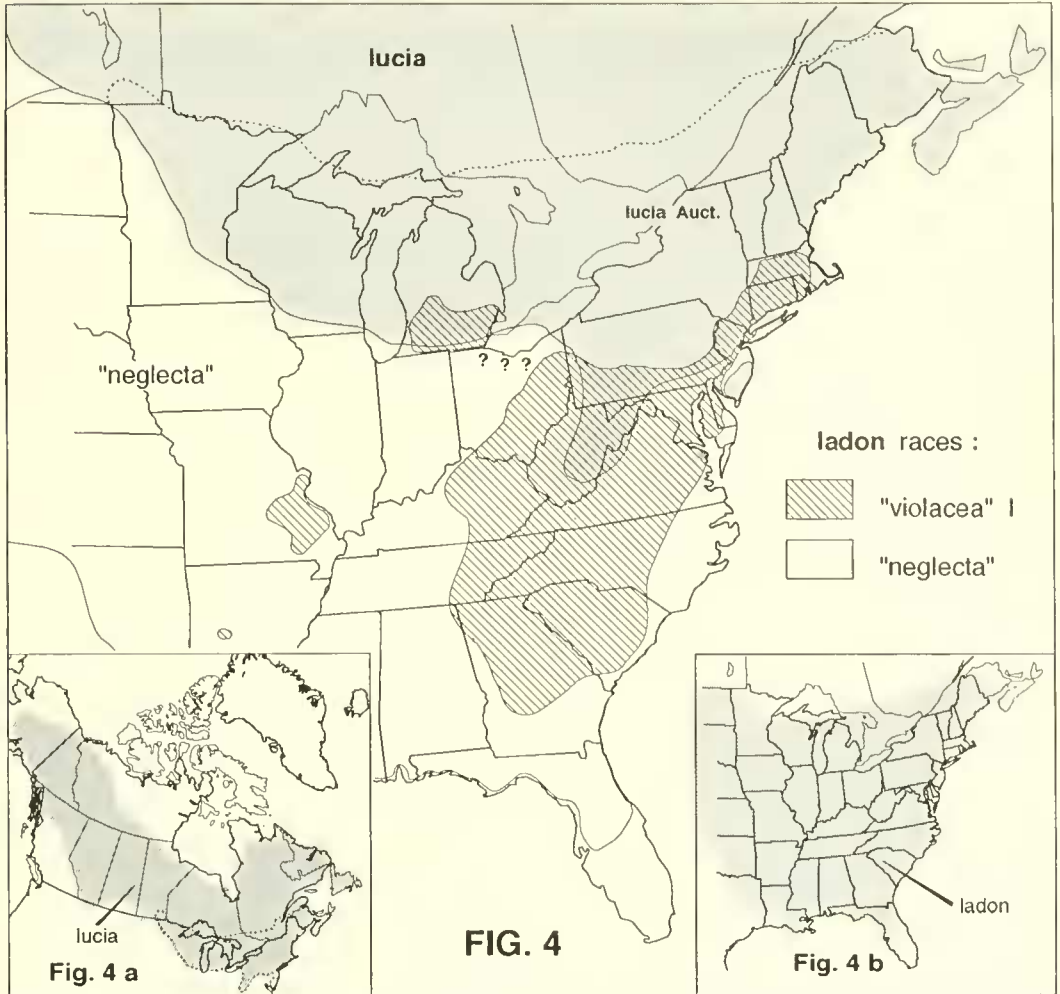
Fig. 4. Map of eastern North America showing the geographic ranges of *Celastrina l. lucia* (including *lucia Auct.* below dotted line) and races "violacea" l and "neglecta." 4a (inset), Map of North America showing entire range of *C. l. lucia*. 4b (inset), Map of eastern North America separately showing range of *C. l. ladon*.

kota. *Celastrina l. argentata* is restricted to the plains in southern Manitoba and Saskatchewan.

The only western taxon that is not allopatric to the other subspecies is "bakeri" (formally a subspecies). All known "bakeri" records occur within the blend zone of subspecies *echo* and *nigrescens*. We consider "bakeri" to be a form of *echo* and *nigrescens* and follow Miller and Brown (1981) in this regard. The distinguishing character of form

"bakeri" is the basal greenish tint on the ventral wing surfaces. This character is also weakly expressed in even some southern populations of *echo*.

Subspecies *lucia* (Fig. 4a) occurs widely throughout the subarctic from Alaska to Labrador then south to Alberta, Saskatchewan, Manitoba, southern Ontario, and Quebec. Traditional ssp. *lucia* Kirby is a very small single-brooded butterfly with very light blue dorsal color tending toward green-
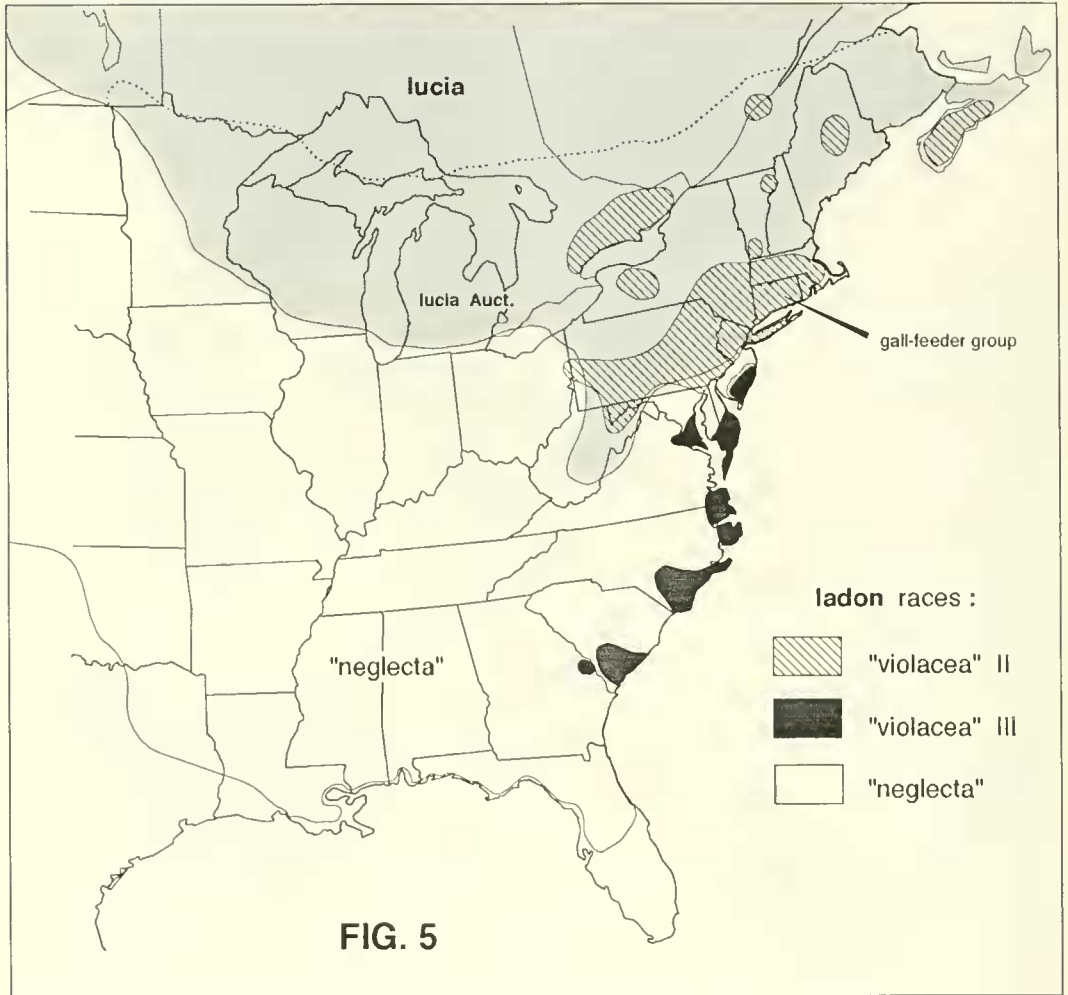
Fig. 5.   Map of eastern North America showing geographic ranges of *Celastrina l. lucia* and *C. l. ladon* races "violacea" II, "violacea" III, and "neglecta."

ish-blue. Heavily marked forms "lucia," "marginata," and "violacea" are common-place. Further south in southern Ontario, Quebec, northcentral and northeastern United States (below dotted line in Fig. 4), *lucia* Kirby is replaced by larger, highly variable specimens of a single early spring brood. The dorsal colors of the latter group are quite polymorphic. Forms "lucia," "marginata," and "violacea": occur, but "marginata" and "violacea" become more frequent near the southern extent of the range (including central Appalachian Mts.). Previous authors have recognized the differences between *lucia* Kirby and the second group in northeastern United States and referred to the latter as "*lucia*" of authors (Klots 1951, Forbes 1960). Confusion has existed regarding their assignment to ssp. *lucia* or to ssp. *ladon*. Through morphological and biological characters we include them with ssp. *lucia* under the designation *lucia Auctorum*.

The known host plants of the different

Celastrina are listed in the Appendix. Larvae of the western subspecies feed on a broad variety of plant families: primarily Asteraceae, Ericaceae, Fabaceae, Polygonaceae, Rhamnaceae, Rosaceae, and Saxifragaceae. The hosts of *argentata, gozora,* and *nigrescens* are not known. *Celastrina l. lucia* is recorded on *Vaccinium* and *Ledum* species (Ericaceae) in the West, but in the East it used those genera and also *Viburnum* (Caprifoliaceae) and *Prunus* (Rosaceae).

Forms and races of *Celastraina ladon ladon*

Subspecies *Celastrina l. ladon* readily divides into several independent races, which have been classically viewed as variable forms of the same subspecies. Historically, the main forms of ssp. *ladon* in the East were known as "violacea" and "neglecta." For descriptions see, Edwards (1866) ("violacea") and Edwards (1862) ("neglecta").

In eastern North America there are at least three "violacea" races, which here are designated "violacea" types I, II, and III. "Violacea" I conforms to the definition of a host race by Jaenike (1981), since it is sympatric with II and III (as well as race "neglecta") and exhibits a different dorsal scale morphology in regions of sympatry (Table 1). This character (transparent long scales overlapping dorsal blue scales of the male wings) is shared only with *C. nigra.* The ranges of types II and III (which both overlap that of race "neglecta") are not presently known to overlap. They may, however, eventually prove to marginally overlap in Delaware, Maryland, eastern Virginia, or New Jersey (Fig. 5).

The "violacea" races differ in larval food plants: type I ("violacea" Edwards) feeds on *Cornus florida* flowers and fruits throughout most of its range; type II feeds on leaf galls of *Prunus serotina,* induced by the eriophyid mite *Phytoptus cerasicrumena* Walsh; and type III feeds on male flowers of *Ilex* species (Appendix). In most cases where mature lar-

vae have been field collected and allowed to pupate, the pupae of all three races enter obligate diapause (as do *lucia, nigra,* and *neglectamajor*). In contrast, mature larvae of the sympatric "neglecta" populations following pupation eclose as adults in 8–12 days.

In southeastern Pennsylvania and northern Delaware, and areas northward, "violacea" I larvae feed on flowers of both *P. serotina* and *Viburnum acerifolium.* In these northern areas, *Cornus florida* (the major host of "violacea" I further south) is scarce and declining (Sargent 1905). Larvae of "violacea" II populations are also known to feed locally on *Viburnum* and *Aralia* flowers, but in areas largely north of "violacea" I where coincidentally cherry galls are rarer. "Violacea" I and II can be distinguished easily by adult wing scale morphology (Table 1). Where the two are sympatric, they are generally asynchronous and adults of the flower-feeding populations ("violacea" I) peak seasonally before the gall-feeding populations ("violacea" II).

The present ranges of the three races of "violacea" appear to be primarily parapatric: "violacea" I is in the Appalachians and Ozarks (where it overlaps the range of *C. nigra*); "violacea" II overlaps I in the southern part of its range; and "violacea" III overlaps I on the inner coastal plain (Fig. 4). The range of "violacea" II may prove to be more extensive than that given in Fig. 5 and extend further west and south into the ranges of "violacea" I and III.

The immature stages of "violacea" III have been recorded on four *Ilex* (holly) species (Appendix). Male and female flowers occur on different plants in *Ilex* (dioecious) and in order to determine whether "violacea" III uses one or both sexes, the flowers of more than 20 plants of each sex of *I. glabra* were beaten into a heavy cloth net at Warren Grove, New Jersey, in mid-June, 1991. Interestingly, larvae (n > 20 third and fourth instars) were obtained only from male plants; female plants contained no larvae.

Race "neglecta" occurs throughout most of the East and its range correlates precisely with Fig. 4b. It occurs with the other three "violacea" races, but generally later in the season. It's distinguished from "violacea" races by white scale insuffusion into the dorsal blue scales of the male wings (Table 1). "Neglecta" differs from *C. neglectamajor* only in the maximal size of the adults and several minor features (Table 1). There are also populations of "neglecta" which share the same larval host (*Cimicifuga racemosa*) with *C. neglectamajor*, adding to the difficulty in their identification. However, they do differ in first instar characters which supports their separate species status. *Celastrina neglectamajor* first instars are yellow, while all *C. ladon* (including race "neglecta" on *Cimicifuga racemosa*) are green. The primary dorsal setae on meso/metathorax are also shorter in *neglectamajor* first instars. *Celastrina neglectamajor* larvae can successfully develop on host *Cimicifuga* leaves, while these leaves appear to be toxic to "neglecta" larvae. Lastly, the two *Celastrina* on *Cimicifuga racemosa* also differ in their seasonal occurrence; larvae of *C. neglectamajor* generally occur earlier than those of race "neglecta" on *Cimicifuga racemosa*, since their adults fly earlier. In the northern part of its range, race "neglecta" does not appear until late spring or summer after the flights of the spring taxa are over. In the southern part of the range, however, "neglecta" is multibrooded (including spring and summer broods).

Celastrina l. ladon is the only subspecies known to extensively overlap other *C. ladon* subspecies in North America. As race "neglecta", *C. l. ladon* overlaps *C. l. sidara* in north central Colorado (Fig. 3), and as several other races, it also overlaps *C. l. lucia* in the northeastern portion of its range (Figs. 4, 5). The ranges of "violacea" II and "neglecta" broadly overlap *lucia* in the Northeast, and "violacea" III (another *ladon* race) occurs with *lucia* in southern New Jersey. These races of *C. l. ladon* are seasonally isolated from *C. l. lucia*, since their adults generally occur later in the season.

DISCUSSION

Ancestral *celastrina* is believed to have entered North America from Eurasia during a period when the Bering land bridge joined North America and Siberia (Eliot 1973). Most of the diversity of the Lycaenopsis section of the Polyommatini (blues), including *Celastrina* Tutt, occurs in the Oriental region (Eliot 1973, Eliot and Kawazoe 1983). In the Orient there are 14 *Celastrina* species, while in North America there are only three species which up to recently were all considered conspecific with Eurasian *C. argiolus* (Scott 1986, Eliot and Kawazoe 1983).

Within the Eurasian *Celastrina*, *C. argiolus* seems most closely related to the North American *Celastrina* because of its distribution in northern latitudes and morphological similarities with many North American taxa. It follows that the North American taxon most closely resembling *argiolus* may therefore be a direct descendent of the ancestor which crossed the Bering land bridge (Beringia). The range of subspecies *lucia* extends closest to present-day Beringia, but *lucia* has a distinctive wing morphology with no characters shared with any Eurasian *Celastrina*, and thus appears to be an unlikely ancestor (Eliot & Kawazoe 1983). On the other hand, the western subspecies *echo* is considerably more similar to *C. argiolus* in wing morphology and coloration. Within the range of *echo* there are populations in which the form "bakeri" (recognized by greenish tint on basal ventral wing surfaces) are common. The "bakeri" character is also particularly strong in the nominate European subspecies *C. a. argiolus* (Higgins and Riley 1975). In both Eurasia and western North America, we suspect the "bakeri" character is a retained plesiomorphy shared with the original North American ancestor.

It is interesting that the greatest species diversity in North American *Celastrina* (3

species) occurs in the East, and in contrast only one is recognized in the West. If the primitive North American *Celastrina* taxa are currently distributed in western North America, why didn't additional species evolve in the West? Similar biogeographic patterns have been made in the distributions of other North American butterflies (Howe 1975). Such stereotypical patterns suggest that the *Celastrina* ancestor that crossed the Bering land bridge into North America moved into the West before entering the East. If this is true, a paradox exists in that western *Celastrina* despite a longer chronology in North America have a smaller species diversity than their eastern counterparts. It is yet possible that some or all of the western subspecies are distinct species. Allozyme studies are in progress to investigate this possibility.

The different degree of host specialization between eastern and western *Celastrina* may help explain the greater species diversity in the East. Larvae of all western taxa, as far as currently known, utilize the flower buds of multiple plant families in a single locality (polyphagy). Eastern taxa in general are host specific at any given locality. Only one eastern race ("neglecta") uses more than one host in a single locality, and yet it is asynchronous to all other sympatric races. *Celastrina l. lucia* uses more than one host in the East, but these hosts generally bloom at the same season and only one host is used in a single locality (usually either *Vaccinium* or *Viburnum*).

The entire group of eastern *Celastrina* species and races are adapted to host plants with seasonally limited resources (flower buds or young shoots). This host specialization may have selected for asynchrony between the species and races. An asynchronous mechanism inducing genetic isolation appears likely for *lucia*, "violacea" I, II, and III, "neglecta," and *neglectamajor* since they occur asynchronously to one another in nature in many localities in the East. In general, *lucia* adults occur first followed in order by "violacea" I and *nigra*, "violacea" II and III, *neglectamajor*, and finally "neglecta."

Only two *Celastrina* are broadly sympatric and synchronic in the East (*C. nigra* and "violacea" I). These two, however, are genetically isolated through their association with different hosts and habitats. Individuals of both taxa intermingle away from their corresponding habitats at mud puddles, but they are almost always males; female *Celastrina* and females of most other blues are rarely encountered at mud puddles (Scott 1986). The females of *nigra* and "violacea" I prefer habitats which correspond to their host's habitat. *Celastrina nigra* females prefer low vegetation along north-facing slopes and shady creek bottoms where *Aruncus dioicus* grows, whereas "violacea" I females prefer flying among the subcanopy tree tops of woodland *Cornus florida*. Male mate-searching behaviors of these *Celastrina* seem to coincide with their conspecific female behavior, so that opposite sexes of the two taxa rarely if ever encounter each other.

The relationship between spring *lucia* and "violacea" I is unclear. They differ in mean eclosion times under laboratory conditions (diapause intensity) (Pratt and Wright, in prep.). They should be asynchronous when in sympatry. They are generally allopatric, but come into contact in southern New England and southern Michigan where intermediate populations are present. At Kingston, Rhode Island, "violacea" I populations (det. by scale morphology) utilize *Vaccinium corymbosum* (a *lucia* host) and exhibit the unique VHW markings of *lucia*. These may be hybrid populations.

Race "neglecta" occurs through most of the East, from central Florida to southern Canada (Fig. 4b) and west to eastern Colorado and North Dakota (Fig. 3). From the southcentral Appalachians to southern New England, it is often abundant in locations where "violacea" I, II, III, and *lucia* were present during earlier months. Since its flight period follows the others, it would seem rea-

sonable that it could have been formed from offspring of the spring races. However, most field-collected mature larvae of the spring races enter obligate diapause, indicating they are probably univoltine. Field-collected mature "neglecta" larvae (n > 430) from southeastern Pennsylvania and Delaware of the "neglecta" first brood did not enter diapause, indicating "neglecta" is multivoltine in summer at this latitude. In some areas where summer "neglecta" occurs, the spring races are scarce to absent and therefore could not have formed the abundant summer "neglecta"; and, vice versa, in some localities the spring races are abundant, but the summer "neglecta" populations are scarce to absent (Shapiro 1966, 1970, 1973, Pratt, Wright, and Pavulaan, pers. obs.).

Conclusion

North American *Celastrina* probably evolved from an *argiolus*-like Eurasian ancestor which crossed the Bering land bridge. Western North American *Celastrina* have segregated into several subspecies, while eastern *Celastrina* have achieved greater diversity through speciation and formation of several races. The eastern diversification most likely was faciliated through host shifts onto plants with seasonally limited nutritional resources. This in turn selected for asynchrony in adult emergence. Gene flow between races may be limited, since: (1) spring races are univoltine, (2) adult emergence in nature coincides with the short blooming periods of their hosts, and (3) adults are short-lived. In general, the flight (esp. males) of one race does not seasonally overlap that of the next. *Celastrina nigra* and "violacea" I are the only sympatric *Celastrina* which do not conform to this asynchronous model. They instead exhibit shifts in habitat preference, which has probably limited gene flow between them.

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Appendix. Host plants of *Celastrina* of North America.

Taxa	Host[a]
C. nigra (= *ebenina*)[b]	*Aruncus dioicus* (13) (young shoots, leaves, and flowers)
C. neglectamajor	*Cimicifuga racemosa* (12) (flower buds & leaves)
C. ladon (Western ssp.)	
cinerea	*Ceanothus fendleri* (14), *Chamaebatiaria millefolium* (13), *Eriogonum wrightii* (11), *Holodiscus* sp. (13), *Lupinus* sp. (8), and *Petrophytum caespitosum* (13)
gozora	Unknown
echo	*Adenostoma fasciculatum* (13), *Baccharis glutinosa* (4), *Ceanothus leucodermis* (14), *C. palmeri* (14), *Heteromeles arbutifolia* (13), *Holodiscus* sp. (13), *Lotus scoparius* (8), *Prunus ilicifolia* (13), and *Spiraea* sp. (13)
nigrescens	Unknown. Perhaps *Prunus virginiana* and other *Prunus* sp. (13)
sidara	*Ceanothus fendleri* (14), *Cornus stolonifera* (6), *Holodiscus* sp. (13), *Jamesia americana* (15), *Physocarpus monogynus* (13), and *Prunus virginiana* (13)
argentata	Unknown
lucia	*Ledum* sp. (7), esp. *L. palustre,* and *Vaccinium* sp. (7)
C. ladon (eastern ssp. and races)	
lucia	*Ledum* sp. (7), esp. *L. palustre, Vaccinium corymbosum* (7), *Viburnum cassinoides* (5)
lucia	*Prunus serotina* (13), *Prunus virginiana* (13), *Rhamnus* sp. (14), *Vaccinium corymbosum* (7), *Viburnum cassinoides* (5), *V. lentago* (5), *V. prunifolium* (5), and *Lonicera tatarica* (5)
"violacea" I	*Cornus florida* (6), *Prunus serotina* (13), *Viburnum acerifolium* (5), and *V. prunifolium* (5)
"violacea" II	*Prunus serotina* (13) (mite galls), *P. virginiana* (13) (mite galls), *Viburnum lentago* (5), and *Aralia hispida* (3)
"violacea" III	*Ilex glabra* (2) (male flowers), *I. laevigata* (2) (male flowers), *I. opaca* (2) (male flowers), *I. vomitoria* (2) (ovip. on male plant)
"neglecta"	*Actinomeris alternifolia* (4), *Agastache nepetoides* (9), *Aralia spinosa* (3), *A. nudicaulis* (3), *Ceanothus americanus* (14), *C. ovatus* (14), *Cimicifuga racemosa* (12), *Collinsonia canadensis* (9), *Cornus alternifolia* (6), *C. stolonifera* (6), *C. racemosa* (6), *C. foemina* (6), *C. amomum* (6), *Erythrina herbacea* (8), *Eupatorium perfoliatum* (4), *Humulus lupulus* (10), *Lupinus argenteus* (8), *Rhus glabra* (1) (flower stalks), *Spiraea latifolia* (13), *Viburnum dentatum* (5)

[a] Flowers and fruits except where indicated. The families in parentheses are 1 = Anacardiaceae, 2 = Aquifoliaceae, 3 = Araliaceae, 4 = Asteraceae (Compositae), 5 = Caprifoliaceae, 6 = Cornaceae, 7 = Ericaceae, 8 = Fabaceae, 9 = Labiatae, 10 = Moraceae, 11 = Polygonaceae, 12 = Ranunculaceae, 13 = Rosaceae, 14 = Rhamnaceae, 15 = Saxifragaceae.

[b] We consider *Celastrina ebenina* Clench (Clench 1972) to be a junior synonym of *Celastrina nigra* (Forbes) (Forbes 1960).